EFFECTS OF CLIMATE VARIABILITY AND FISHING ON GADID-CRUSTACEAN INTERACTIONS IN SUBARCTIC ECOSYSTEMS

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A

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Abstract

Snow crab (*Chionoecetes opilio*) are a vital economic and biotic resource to many subarctic ecosystems. Their abundance varies greatly, but what causes large changes in production and early life survival is unknown. My overall goal is to improve our understanding of snow crab population dynamics during early life history stages. Chapter 1 provides background information on subarctic ecosystems, addresses possible mechanisms of population control and potential drivers of variability, describes snow crab life history, and reviews recent population trends in snow crab and their major cod predators. Chapter 2 details a regression study examining the effects of snow crab spawning stock biomass, environmental conditions, and Pacific cod (*Gadus macrocephalus*) or Atlantic cod (*Gadus morhua*) biomass on snow crab recruitment. This study compares three ecosystems: the eastern Bering Sea, the Newfoundland-Labrador Shelf, and the southern Gulf of St. Lawrence. Cold ocean conditions during early life history were associated with increased snow crab recruitment or recruitment indices in all three ecosystems. However, there was no consistent observed effect of spawning stock biomass or gadid predation on subsequent recruitment. The dominant role of environmental conditions in driving snow crab recruitment highlights the importance of an ecosystem-based management approach for these stocks.

Table of Contents

Page

Signature Page i

Title Page ii

Abstract iii

Table of Contents iv

List of Figures vii

List of Tables viii

Acknowledgements ix

General Introduction 1

References 5

Chapter 1: Dynamics of gadoids and crustaceans in subarctic ecosystems 7

1.1 Introduction 7

1.2 Subarctic Ecosystems 7

1.3 Population Control Mechanisms 8

1.4 Drivers of Variability 9

1.4.1 Climate 10

1.4.2 Biotic Interactions 11

1.4.3 Fishing 14

1.5 Physical Setting 15

1.5.1 Eastern Bering Sea 15

1.5.2 Gulf of St. Lawrence 16

1.5.3 Newfoundland/Labrador Shelf 17

1.5.4 Physical Setting Summary and Comparisons 18

1.6 Snow Crab 18

1.6.1 Life Cycle 19

1.6.2 Diet, Predators, and Parasites 20

1.6.3 Snow Crab Population Trends 22

1.6.4 Management 23

1.7 Gadoid Fishes 23

1.7.1 Gadid Population Trends 24

1.8 References 26

Tables 33

Figures 35

Chapter 2: Effects of temperature and gadid predation on snow crab recruitment: Comparisons between the Bering Sea and Atlantic Canada 38

Abstract 38

2.1 Introduction 39

2.2 Methods 41

2.2.1 Study areas 41

2.2.2 Data 42

2.2.2.1 Snow crab data 42

2.2.2.2 Environmental data 44

2.2.2.3 Predators 45

2.2.3 Analytical approach 46

2.3 Results 50

2.4 Discussion 53

2.4.1 Overview 53

2.4.2 Environment, spawning stock biomass, and predation 54

2.4.3 Implications for stock assessment and management 60

2.5 Acknowledgements 61

2.6 References 62

Tables 67

Figures 70

General Conclusions 74

References 79

List of Figures

Page

Chapter 1:

Figure 1.1 Snow crab population trends 35

Figure 1.2 Catches of Pacific and Atlantic cod (1000 t) 36

Figure 1.3 Biomass of Pacific and Atlantic cod (1000 t) 37

Chapter 2:

Figure 2.1 Study regions 70

Figure 2.2 Model fits 71

Figure 2.3 Model residuals through time 72

Figure 2.4 Relationship between climate and snow crab recruitment. 73

List of Tables

Page

Chapter 1:

Table 1.1 Types of biotic interactions 33

Table 1.2 Ecosystem overview 34

Chapter 2:

Table 2.1 Explanatory variables and lags used in modeling 67

Table 2.2 Model results with regression coefficients 68

Table 2.3 Comparing ecosystems 69

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General Introduction

This study is a contribution to the international Ecosystem Studies of Sub-Arctic Seas (ESSAS) program, which aims to understand how climate changes affect subarctic ecosystems (Hunt & Drinkwater 2005). The program has several working groups, each focusing on different aspects of subarctic systems from climate drivers to lower trophic level variability and fishes. Working Group 4 on "Climate Effects at Upper Trophic Levels" aims to, "assess the effects of ocean climate variability and fishing on the interactions between gadoid fishes and crustaceans by conducting a comparative study across multiple sub-arctic marine ecosystems" (McBride 2008). Gadoid fishes and crustaceans are significant components of many subarctic ecosystems. These species are integral parts of subarctic food webs (Aydin et al. 2007) and their presence supports some of the most important commercial fisheries in subarctic regions (Hunt & Drinkwater 2007). Successful management of gadid and crustacean fisheries in a changing climate requires a better understanding of the effects of climate variability on these stocks, on interactions among stocks, and on the ecosystems in which they are embedded. My thesis contributes to this understanding and to the goals of ESSAS by examining the variability in several crustacean stocks relative to climate variability and gadid abundance.

Climate variability may have major effects on crustacean and gadids. This link is supported by statistical analyses that show strong relationships between climate and the recruitment or abundance of various crustaceans (Rosenkranz et al. 2001, Ouellet et al. 2007, Dawe et al. 2008, Koeller et al. 2009) and gadid stocks (Hollowed et al. 2001, Beaugrand et al. 2003, Mueter et al. 2006). One general hypothesis is that gadoid fishes

and crustaceans respond in opposite ways to variation in ocean climate and that climate variation may account for some of the changes in productivity or abundance in these species (Lilly et al. 2000).

Another factor that may influence gadid and crustacean demographics is predation. For example, a release from predation may explain the large increases in snow crab (*Chionoecetes opilio*) and northern shrimp (*Pandalus borealis*) populations that coincided with the dramatic crash of the Atlantic cod (*Gadus morhua*) population along the Newfoundland-Labrador Shelf (Link et al. 2009). Predation may have also played a role in restructuring the Gulf of Alaska ecosystem in the late 1970s when fishes replaced crustaceans as the dominant taxa (Anderson & Piatt 1999). While warming ocean climate may have prompted the initial decline of northern shrimp, concurrent increases in groundfish populations may have imposed additional mortality on this species (Anderson & Piatt 1999). A second general hypothesis proposes that changing predation pressures can help to explain negative associations between gadoid fishes and crustaceans (Lilly et al. 2000).

Many prior studies have focused on specific ecosystems to examine the responses of crab, shrimp, and cod populations to altered climate or predation pressures. However, the responses of gadoid fishes and crustaceans to changing conditions may vary among different ecosystems. To better understand key processes and drivers, ESSAS (Megrey et al. 2009) and others (Alheit et al. 2010, Murawski et al. 2010) advocate a comparative approach across multiple ecosystems. Following this line of reasoning, I conducted comparative analyses within and among a number of subarctic ecosystems to identify the

most important factors regulating interactions between gadids and crustaceans and their population dynamics. Specifically, I focused on snow crab and the major gadids that prey on them and evaluated results to see whether estimated effects are similar across ecosystems.

The overall goal of my thesis is to improve our understanding of snow crab population dynamics in subarctic ecosystems. I focused on early life history stages because snow crab recruitment is thought to drive overall population variability. Recruitment in all stocks shows tremendous year-to-year fluctuations, but it is unclear what causes this high variability. Recruitment levels may vary because of biotic interactions, environmental pressures, and/or changes in spawning stock biomass. The extent to which any of these factors determine snow crab recruitment may vary among ecosystems. In chapter 1, I summarize general characteristics of subarctic ecosystems, describe the specific study areas used in chapter 2, review concepts relating to biotic and abiotic interactions, and provide some background information on snow crab and their gadid predators. The second chapter uses a regression approach to model snow crab recruitment (to a specific size class) in three subarctic ecosystems: the eastern Bering Sea, the Gulf of St. Lawrence, and the Newfoundland-Labrador Shelf. By addressing the following questions I hope to explain observed changes in snow crab year-class strength:

1) Does snow crab recruitment show an inverse relationship with the biomass of gadid predators?
2) Is snow crab recruitment significantly related to temperature or to other key climate variables?

3) What effect does adult spawning stock biomass have on future snow crab recruitment?
4) Do snow crab show similar relationships with biotic and environmental variables across systems?

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Chapter 1: Dynamics of gadoids and crustaceans in subarctic ecosystems

1.1 Introduction

In Chapter 2, I relate snow crab (*Chionoecetes opilio*) recruitment to predation by gadoid fishes, environmental conditions, and parental stock effects in several subarctic ecosystems. In order to better understand that research, I present key background information here. I first introduce subarctic ecosystems and the various population control mechanisms and drivers of population variability that may act within them. Then, I provide a brief overview of the ecosystems used in Chapter 2. I conclude with an overview of snow crab and the two cod species.

1.2 Subarctic Ecosystems

A number of characteristics differentiate subarctic ecosystems from other marine ecosystems. Subarctic ecosystems generally experience a high degree of seasonality in ice cover and sunlight and large influxes of freshwater (Hunt & Drinkwater 2007). Subarctic marine fauna are characterized by a relatively low level of biodiversity typically dominated by a few very abundant species. Many of these systems currently support or once supported large gadid stocks (Hunt & Drinkwater 2007), as well as seasonally high abundances of seabirds and marine mammals (Sakurai 2007).

Gadoid fishes and crustaceans are among the most important commercially harvested species in subarctic ecosystems. For example, in 2009 eastern Bering Sea landings were valued at a total ex-vessel value of 183 million US dollars (USD) for red king crab (*Paralithodes camtschaticus*), snow crab, and Tanner crab (*Chionoecetes*

bairdi) (Alaska Department of Fish and Game 2010) and 381 million USD for the two major gadids, walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*) (Hiatt et al. 2010).

1.3 Population Control Mechanisms

Several general mechanisms of population control have been proposed to explain variability in species abundance and community composition, including top-down, bottom-up, and wasp-waist control (Worm & Myers 2003, Hunt & McKinnell 2006). In bottom-up control, resource limitation is the primary regulator of species abundances, and species abundance at a lower trophic level has the greatest influence on abundances at higher trophic levels. Since both predator and prey species depend on the availability of resources, predator and prey abundances are expected to be positively correlated. In contrast, top-down control is a consumer-driven process where predation pressures from higher trophic levels are the main regulator of species abundances. If top-down control is driving a system, then predator and prey abundances should be negatively correlated. Wasp-waist control may occur in systems where one or a few species dominate the mid-trophic levels. Under this situation mid-trophic level species' abundances drive the abundances of species at both higher and lower trophic levels. It is important to note that these types of control are not mutually exclusive. Both bottom-up control and top-down control can act on the same species but on different spatial or temporal scales. Bottom-up controls may structure species distribution and abundance on a large geographic scale, while top-down controls tend to act on a localized scale reflecting the limited or patchy

distribution of most predators (Worm & Myers 2003, Hunt & McKinnell 2006). Moreover, ecosystems are dynamic and the mechanism of population control that is most important may change over time. For example, the oscillating control hypothesis for the southeastern Bering Sea predicts that during cold climate regimes bottom-up controls predominate while during warm regimes top-down controls prevail (Hunt et al. 2002).

The type of mechanism driving a species' abundance and distribution has implications on commercial harvesting strategies. If a population is regulated by bottom-up controls, then when some individuals are removed from a population during a commercial fishery, the remaining individuals may be able to compensate for this loss owing to increased survival and/or growth as a result of increased per-capita resource availability (Hunt & McKinnell 2006). This is the implicit assumption of most single-species approaches to management. However, when top-down controls prevail, increased fishing on a prey species can lead to further declines because the remaining individuals will be more susceptible to predation pressures (Hunt & McKinnell 2006). Such interactions are increasingly considered under ecosystem-based approaches to fisheries management.

1.4 Drivers of Variability

The abundance, distribution, or fitness of a given cohort or population is influenced by a triad of drivers acting at multiple spatial and temporal scales: climate variation, biotic interactions, and fishing (Link et al. 2010). Identifying the main drivers impacting the demographics of commercially exploited populations is critical to

evaluating the effects of management actions. However, distinguishing the effects of climate, biotic interactions, and fishing is often difficult due to data limitations (Hamilton 2007) and may not even be possible if the effects are non-additive (Planque et al. 2010).

1.4.1 Climate

Climate has long been recognized as one of the primary drivers of variability in fish populations (Cushing 1982). Despite this recognition, the specific mechanisms linking climate to higher trophic levels are often unknown or unsupported by research (Drinkwater et al. 2010). However, if climate plays a large role in regulating populations, significant correlations between biological and environmental variables should be seen (Worm & Myers 2003). Indeed, climate variability has been correlated with the recruitment and abundance of both crustaceans (Rosenkranz et al. 2001, Ouellet et al. 2007, Dawe et al. 2008, Koeller et al. 2009) and gadid stocks (Hollowed et al. 2001, Beaugrand et al. 2003, Mueter et al. 2006), and the two groups have been hypothesized to respond in opposite ways to environmental influences including temperature (Lilly et al. 2000). For example, along the Newfoundland-Labrador Shelf cold conditions seem to be favorable for crustaceans including northern shrimp (Parsons & Colbourne 2000) and snow crab (Dawe et al. 2008). In contrast, warm conditions seem to favor the survival of Atlantic cod (*Gadus morhua*) through early life stages in the subarctic regions of the North Atlantic near the cold limit of their distribution (Planque & Frédou 1999, Ottersen et al. 2006).

Species-environment interactions are typically much more complex than assumed by statistical analyses based on linear correlations or regressions. Biological responses to changing climate conditions can be nonlinear (Cury et al. 1995, Mueter et al. 2006) and non-additive in nature (Ciannelli et al. 2007, Ciannelli et al. 2008). Species responses to changing climate conditions can also exhibit a threshold response where once a threshold value is reached, a population responds drastically to a relatively slight change in environmental conditions (Ciannelli et al. 2007). Therefore, in Chapter 2, I considered potential non-linearities in the effects of climate on biological populations using appropriate statistical techniques.

1.4.2 Biotic Interactions

Intra- and interspecific interactions between organisms can be described by their effects on net fitness (Table 1.1). Here, I focus on predator/prey and competitive interactions, in which individuals of at least one species lose fitness (Wootton 1998). In predator/prey interactions the predator typically profits while the prey experiences a loss of fitness (Wootton 1998). Predator/prey interactions occur both between species (predation) and within a single species (cannibalism). Snow crab are vulnerable to both.

Prey species often exhibit life history adaptations that minimize predation by physically separating vulnerable life stages from potential predators. Juvenile nursery areas are commonly located in shallow, nearshore areas away from large predators, though predator avoidance is not the sole reason for their location. Highly mobile prey may be able to minimize predation by migrating away from their predators. Evidence

indicates that snow crab may migrate to shallow waters (Chabot et al. 2008), and capelin (*Mallotus villosus*) may migrate to "thermal refuge areas" (Rose & Leggett 1990) to avoid high densities of Atlantic cod.

The effects of predation are a function of the predator's diet preferences and of the size of both predator and prey. Chabot et al. (2008) studied how size influenced the predator-prey relationship between Atlantic cod and snow crab in the Gulf of St. Lawrence. The importance of snow crab to the diet of Atlantic cod increased with cod length up to about 70-80 cm fork length and then declined. Most of the snow crabs consumed were of an intermediate size, and these crabs were more energetically profitable to Atlantic cod than those of smaller or larger sizes (Chabot et al. 2008). These size-based relationships imply that studies of predation need to account for the relative sizes of predators and prey in addition to their abundances.

Cannibalism is common in snow crab and is hypothesized to play an important role in regulating cohort strength (Lovrich & Sainte-Marie 1997, Squires & Dawe 2003). As with interspecific predation, the importance of cannibalism varies with the size of the consumer and prey individuals (Lovrich & Sainte-Marie 1997). Field studies examining snow crab stomach contents show that the early benthic stages of snow crab are most vulnerable to predation by conspecifics in both the Newfoundland-Labrador Shelf (Squires & Dawe 2003) and Gulf of St. Lawrence regions (Lovrich & Sainte-Marie 1997). Cannibalism may occur within a cohort or between cohorts with larger, older individuals preying on smaller, younger ones (Wootton 1998). For snow crab, a

laboratory experiment suggests that intercohort predation has a greater influence on year class strength than competition within a cohort (Sainte-Marie & Lafrance 2002).

Competition results when an individual has diminished access to a critical resource due the presence of a competitor and results in a loss of fitness for both individuals involved. There are two main types of competition: exploitative competition and interference competition. Exploitative competition is indirect and occurs when a competitor depletes the availability of a limited resource for another competitor (Wootton 1998). This can occur when one individual uses a renewable resource or inhabits an open space (Ricklefs & Miller 2000). Interference competition occurs between individuals in direct spatial contact when the behavior of one organism limits the ability of another to access a resource (Wootton 1998) creating a relative resource shortage (Ricklefs & Miller 2000). Newly settled snow crab may compete for food and space if nursery areas are crowded (Sainte-Marie & Lafrance 2002).

Considerations of spatial scales can affect our ability to identify predator/prey and competitive interactions (Ciannelli et al. 2008). On large scales, densities of the populations involved tend to be positively correlated due to similar resource preferences or due to predators assembling in areas where prey are present. However, on small spatial scales negative correlations emerge due to local competition, prey consumption, or predator avoidance. A population's geographic distribution may change with ontogeny (Sainte-Marie et al. 2008) or on multi-year or seasonal scales (Zheng & Kruse 2006) thus altering the opportunities for populations to interact. Chapter 2 uses a broad comparative approach to consider interactions at the ecosystem level. Small-scale and

temporally changing spatial dynamics are beyond the scope of my research, though they may be locally important.

1.4.3 Fishing

Fishing affects populations directly through mortality and indirectly by altering the age/size structure of populations and the quality of their environment. I briefly discuss four examples of indirect fishing effects: habitat modifications, changes to population size structure, altered geographic distributions, and release from competition or predation. First, benthic habitat and community structure can be altered by certain fishing practices, such as bottom trawling (Thrush et al. 1998), thereby changing biotic interactions. Second, commercial fishing gear usually targets and removes the largest individuals from a population thereby truncating size and age structure (Planque et al. 2010). In a species where large or old individuals have the highest reproductive potential, a size selective fishery may increase a population's susceptibility to climate variation (Ottersen et al. 2006, Hamilton 2007, Hsieh et al. 2008, Planque et al. 2010). Third, commercial fishers target certain geographic areas more than others (Planque et al. 2010). So, fishing can constrict a population's geographic distribution to a smaller region and this loss of spatial heterogeneity can increase a population's vulnerability to climate changes (Hsieh et al. 2008). Fourth, fisheries can alter biotic interactions by allowing a non-target species to extend their ranges following the removal of a predators or competitors (Botsford et al. 1997). Clearly, because fishing can alter responses to the other drivers of variability, namely climate and biotic interactions, fishing effects cannot

be considered in isolation. These other drivers must be considered in the context of historical and current fishing practices.

1.5 Physical Setting

In Chapter 2, I modeled snow crab recruitment in areas within three large marine ecosystems: the eastern Bering Sea, the Gulf of St. Lawrence, and the Newfoundland-Labrador Shelf. Below I describe the physical setting of each of these ecosystems.

1.5.1 Eastern Bering Sea

The eastern Bering Sea has a shallow, broad continental shelf extending from the coastline to the shelf break at roughly 180 m (Hunt & Megrey 2005). The shelf is partitioned into three regions based on differences in depth and hydrographic conditions: the Inner Domain (0-50 m depth), the Middle Domain (50-100 m depth), and the Outer Domain (100 m to the shelf break) (Hunt & Megrey 2005).

Current flows in the eastern Bering Sea are dominated by the Alaska Stream and the Alaska Coastal Current, which enter the region through numerous Aleutian Island passes (Stabeno et al. 1999, Hunt & Megrey 2005). After entering the eastern Bering Sea, waters of the Alaska Stream form the Aleutian North Slope Current, much of which branches off to form the Bering Slope Current that flows northwest along the shelf break (Stabeno et al. 1999). The Alaska Coastal Current enters the Bering Sea through Unimak Pass and continues northward on the shelf, eventually traveling through Bering Straight into the Chukchi Sea (Stabeno et al. 1999).

Ice cover in the eastern Bering Sea is highly seasonal (Hunt & Megrey 2005, Mueter et al. 2009); up to 75% of the shelf may be covered by sea ice from late fall to early spring (Niebauer et al. 1999, Orensanz et al. 2004). On a seasonal basis, the ice edge moves an average of 1700 km as the ice expands and contracts (Niebauer et al. 1999, Orensanz et al. 2004). As the ice retreats, it leaves behind low salinity water that becomes heated and stratifies the water column. On the bottom is the higher salinity cold pool (< 2° C), which can occupy the middle shelf domain throughout summer and limit the distribution of temperate species (Orensanz et al. 2004).

1.5.2 Gulf of St. Lawrence

The Gulf of St. Lawrence opens to the Atlantic Ocean at just two locations: the Strait of Belle Isle in the northeast, and Chabot Straight in the southeast (Han et al. 1999). This semi-enclosed sea has both shallow areas and deep channels. The prominent Laurentian Channel extends from the St. Lawrence Estuary through Chabot Straight (Han et al. 1999). Other major features include the Esquiman and Anticosti channels in the northern Gulf of St. Lawrence and the Magdalen Shallows in the south (Han et al. 1999). The southern gulf has a maximum depth of 130 m but most of the shelf is less than 60 m depth (Morissette et al. 2009).

Atlantic water enters the Gulf of St. Lawrence at depth though the Laurentian Channel (Han et al. 1999), and the Strait of Belle Isle provides a pathway for Arctic water inflow (Han et al. 1999). The Gulf of St. Lawrence also receives a large amount of freshwater input from the St. Lawrence River (Han et al. 1999). Circulation is cyclonic

within the region, although the complex bottom topography alters current flows at a finer scale (Han et al. 1999).

In winter the Gulf of St. Lawrence becomes ice covered and two layers of water can be found, with cool, low-salinity water at the surface and warmer slope-derived water at depth (Han et al. 1999). During spring and summer a warm surface layer forms, displacing the previous cooler surface water downward to form the cold intermediate layer (Han et al. 1999). Since the southern Gulf of St. Lawrence is shallow, this region is cold from the surface to the seafloor during winter and contains only two layers in the summer (the warm surface layer and cold intermediate layer) (Han et al. 1999).

1.5.3 Newfoundland/Labrador Shelf

The Newfoundland-Labrador Shelf off Canada's east coast has a series of nearshore, shallow underwater banks (DFO 2009). Three of these banks are in the study areas considered in Chapter 2: the Belle Isle Bank, Funk Island Bank, and Grand Bank (DFO 2009).

The southward flowing Labrador Current brings cold water to the shelf and is the region's primary circulation feature (DFO 2009). Cross-shelf exchange with warmer continental slope water also influences the nearshore waters of the Newfoundland-Labrador Shelf (DFO 2009).

In winter, inshore areas beneath sea ice tend to be uniformly cold with depth, whereas in offshore areas warm water occurs at depth (Prinsenberg et al. 1997). During

summer, the cold intermediate layer forms over the banks; the area of this layer is larger in years with more sea ice cover (Prinsenberg et al. 1997).

1.5.4 Physical Setting Summary and Comparisons

The eastern Bering Sea in the Pacific Ocean and the southern Gulf of St. Lawrence and Newfoundland-Labrador shelf in the Atlantic Ocean share some commonalities. Each of these subarctic systems experiences some degree of ice cover and has either a cold pool or cold intermediate layer in spring and summer months. However, differences are also apparent. The eastern Bering Sea is higher in latitude than the other two ecosystems (Table 1.2). While the eastern Bering Sea and Newfoundland-Labrador shelf are comparable in size, the southern Gulf of St. Lawrence is more than five times smaller in area (Table 1.2). Current patterns and water sources differ among regions. Warmer water enters the eastern Bering Sea from the south, but colder water enters the Newfoundland-Labrador Shelf from the north. The Gulf of St. Lawrence receives water from both cold northern and warm southern sources. Bathymetry varies among regions, but in Chapter 2 I focus on snow crab, which occur in similar depths on the continental shelves of all three regions.

1.6 Snow Crab

Snow crab are a stenothermic species found along the continental shelf and slope areas in the North Pacific and North Atlantic Oceans (Sainte-Marie et al. 2008). Juveniles and adults inhabit areas with sandy or muddy bottoms in waters ranging from

-1 to 5°C (Fisheries Resource Conservation Council 2005) associated with a cold pool of water (Sainte-Marie et al. 2008). Due to variation in early life production and survival, recruitment is highly variable and cyclic (Sainte-Marie et al. 2008). In the following sections, I describe the life cycle, diet, predators, and population trends for snow crab.

1.6.1 Life Cycle

Snow crab undergo multiple transformations throughout their life cycle. Mature females, after reaching their terminal molt, are classified as primiparous (mating for the first time) or multiparous (having mated before) (Sainte-Marie 1993). Female snow crab are able to store sperm in specialized organs called spermathecae, hence multiparous females may fertilize eggs from sperm reserves instead of mating (Watson 1970). Once fertilized, eggs are carried by the female for roughly one to two years and typically hatch during spring (Moriyasu & Lanteigne 1998). Incubation time is moderated by temperature, taking longer in cooler conditions (Webb et al. 2007, Kuhn & Choi 2011). Embryo development rate also differs between primiparous and multiparous females with shorter development time for the latter (Elner & Beninger 1992, Moriyasu & Lanteigne 1998).

A review of snow crab life history by Kruse et al. (2007) states that after hatching, snow crab go though two zoeal larval stages in the upper mixed layer of the water column before transitioning to megalops larvae and settling to the substrate in early fall. After settlement, megalopae transition to immature juveniles (Dionne et al. 2003). Development varies with sex. Males are classified into three developmental stages:

immature, adolescent, and adult. At the first critical molt, which can occur at 37 (Sainte-Marie et al. 1995) to 41 mm carapace width, immature males transition through puberty to become physiologically mature adolescent males (Hébert et al. 2002). The second critical molt, known as the terminal molt, marks the end of growth (Sainte-Marie et al. 1995). At the terminal molt the chelae (claw) height becomes larger relative to the carapace width and the male becomes a mature adult (previously known as morphometrically mature male) (Sainte-Marie et al. 1995, Hébert et al. 2002). In eastern Canada, the maximum carapace width of males has been estimated at 150 mm (Chabot et al. 2008). Females are classified as either immature or mature based on whether they have reached their terminal molt (Watson 1970), which can occur from 35 mm (Ernst et al. 2005) to upwards of 80 mm carapace width (Ernst et al. 2005, Chabot et al. 2008). Estimates of lifespan indicate that after reaching the terminal molt both sexes of snow crab likely survive no more than 6 years in the Gulf of St. Lawrence (Sainte-Marie et al. 1995) and females survive no more than 7 years in the eastern Bering Sea (Ernst et al. 2005).

1.6.2 Diet, Predators, and Parasites

Snow crab consume a broad range of prey items and their diet changes with age. While larval snow crab primarily consume plankton (reviewed in Kruse et al. 2007), adolescent and adult snow crab are omnivorous. Diet studies of snow crab in Atlantic Canada indicate that fishes, polychaetes, crustaceans, and mollusks are the major components of the diet for these age groups (Wieczorek & Hooper 1995, Squires &

Dawe 2003). However, shrimp (Squires & Dawe 2003), algae, and echinoderms (Wieczorek & Hooper 1995) may be regionally important. Even non-food items such as plastic and metal have been noted in snow crab stomach contents (Wieczorek & Hooper 1995).

Snow crab are eaten by many types of organisms with pelagic predators eating the larval stages and benthic feeders eating the juveniles. Gadoid fishes, salmon, and jellyfish are known to consume larval snow crab (reviewed in Kruse et al. 2007). Groundfish including Pacific and Atlantic cod prey on snow crab throughout their geographic range (Chabot et al. 2008). Several studies show that snow crab juveniles are susceptible to cannibalism by older juvenile cohorts and adults (Lovrich & Sainte-Marie 1997, Sainte-Marie & Lafrance 2002, Squires & Dawe 2003). Eelpouts, sea stars, and octopus have also been documented to eat snow crab juveniles (see Aydin et al. 2007 and references therein).

Disease negative effects snow crab abundance through increased mortality rates. The parasitic dinoflagellate *Hematodinium* sp. causes snow crab to develop bitter crab disease, also known as bitter crab syndrome. Bitter crab disease occurs in both the Pacific (Meyers et al. 1996) and Atlantic Oceans and mortality rates of 100% have been noted in naturally infected crabs (Shields et al. 2005). Bitter crab disease is also seen in Tanner crab, which share the same genus as snow crab (Siddeek et al. 2010). In Tanner crab, Siddeek et al. (2010) found that current management rules are sufficient to account for bitter crab disease in the lightly infected eastern Bering Sea stock, but not in a more

heavily infected stock found in Southeast Alaska. At present, the capability of bitter crab disease to reduce snow crab abundance is not fully understood (Bower et al. 2003).

1.6.3 Snow Crab Population Trends

Many crab species, including snow crab, have fluctuating population levels that are highly sensitive to the incoming recruitment (Zheng & Kruse 2006). I will discuss trends in snow crab populations over the last several decades within each of the study regions.

Since the 1970s the abundance of eastern Bering Sea snow crab has varied substantially with peak abundance in the late 1980s and early 1990s (Fig. 1.1) (Turnock & Rugolo 2010). Following a decline in mature snow crab biomass and landings, the eastern Bering Sea snow crab fishery was declared overfished in 1999 and has been under a rebuilding plan since 2000 (NOAA 2001). The geographic distribution of snow crab in the eastern Bering Sea has contracted and shifted north in recent decades and both Pacific cod predation and northward advection may make it difficult for snow crab to reestablish populations in southern areas (Orensanz et al. 2004).

In both the Gulf of St. Lawrence and Newfoundland-Labrador shelf regions, fisheries for snow crab began in the 1960s and evolved into substantial fisheries during the 1970s (DFO 2010b). In the Gulf of St. Lawrence landings peaked in 1982 then declined until 1990 (DFO 2010b). Biomass was high from 1992-1995, relatively stable from 1997-2007 and has declined in recent years (DFO 2010b). The Gulf of St. Lawrence stock has become increasingly dependent on recruitment rather than standing

biomass (DFO 2010b). Along the Newfoundland-Labrador shelf snow crab populations surged with the crash of Atlantic cod (Link et al. 2009). The exploitable biomass then declined from the late 1990s until the early 2000s but has since increased (DFO 2010a).

1.6.4 Management

A number of measures are used to manage snow crab fisheries in the eastern Bering Sea and in Atlantic Canada. In addition to annual catch limits (total allowable catch), fisheries in each of these regions are subject to sex, size, season, and gear restrictions (DFO 2010a, b, Turnock & Rugolo 2010). Only adult male snow crab may be harvested. In the eastern Bering Sea males must be 78 mm carapace width to be legally harvested; however, because of processor demands the effective minimum size is 102 mm carapace width (NOAA 2001). The minimum size for harvest is 95 mm carapace width in the Gulf of St. Lawrence (DFO 2010b) and Newfoundland-Labrador shelf (DFO 2010a) regions. Season restrictions in the eastern Bering Sea are designed to protect snow crab during molting and mating periods (Turnock & Rugolo 2010). Limits on fishing gear require pots or traps in the eastern Bering Sea (NOAA 2001) and in Atlantic Canada (DFO 2010a, b).

1.7 Gadoid Fishes

Gadoid fishes are common throughout subarctic regions, where they often constitute the majority of fish biomass. In the North Atlantic common gadids include Atlantic cod, haddock (*Melanogrammus aeglefinus*), and saithe (*Pollachius virens*)

(Bogetveit et al. 2008), while Pacific cod and walleye pollock are the most abundant gadids in the North Pacific Ocean (Anderson & Piatt 1999). Atlantic cod and Pacific cod have a broad diet consisting largely of forage fishes, demersal fishes, and crustaceans (Aydin et al. 2007, Link et al. 2009) and among gadids, these two species appear to be the main consumers of snow crab.

1.7.1 Gadid Population Trends

The status of cod populations is quite different between the eastern Bering Sea where Pacific cod biomass has been stable and the two Atlantic Canada regions where cod populations are currently depressed. In the eastern Bering Sea, Pacific cod catches increased in the 1980s and remained stable thereafter (Fig. 1.2). Biomass, which increased following the well-known 1976/77 regime shift in the North Pacific, has been at high levels for the past several decades (Fig. 1.3). In contrast, in the 1990s Atlantic cod stocks in the Gulf of St. Lawrence experienced a large decline (Swain et al. 2009) and the Newfoundland-Labrador cod stock crashed (Link et al. 2009).

Prior to the collapse, Atlantic cod had been harvested for centuries along the Newfoundland-Labrador shelf (Hutchings & Myers 1994). Between the early 1800s and the historic maximum in 1968 the fishery catches increased dramatically from around 100,000 tons to 810,000 tons (Hutchings & Myers 1994). By the late 1970s harvests had declined by roughly 80% from the peak (Fig. 1.2). In the late 1980s and early 1990s the stock crashed (Link et al. 2009), and the Canadian government imposed a commercial fishing moratorium in 1992 (Hutchings & Myers 1994). During that year spawner

biomass was estimated at 22,000 tons, a stark contrast from the 1.6 million tons estimated during the peak. Since the crash the stock has remained depressed at roughly 2% of the level seen in the early 1960s (Link et al. 2009).

Most Atlantic cod stocks have been overfished and are now at low abundance levels (Link et al. 2009). For most stocks smaller body sizes and a contraction in geographic range has accompanied the reduced population size (Link et al. 2009). Because of these biological changes it is unclear whether depressed stocks will respond similarly to climate changes as did larger populations in the past (Link et al. 2009).

1.1.

1.8 References

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Table 1.1 Types of biotic interactions

Effect of on individual from species i on the fitness of individuals of species j ($effect_{i,j}$) and vice versa.

$Effect_{j,i}$	$Effect_{i,j}$		
	+	0	-
+	mutualism	commensalism	predator/prey host/parasite
0	commensalism	neutral	amensalism
-	predator/prey host/parasite	amensalism	competition

Note: Adapted from Wootton (1998) and Ricklefs & Miller (2000). A '+' indicates positive effect on fitness, '-' indicates negative effect, and 0 indicates no effect.

Table 1.2 Ecosystem overview

Summary of latitudes and areas of three marine ecosystems: the eastern Bering Sea (EBS), Newfoundland Labrador Shelf (NL), and the southern Gulf of St. Lawrence (SGSL).

Feature	EBS	NL	SGSL
Latitude (°N)	54.5 – 61.0	42.6 - 55.2	45.6 - 49.2
Approximate Area (km^2)	430,829	388,204	74,137

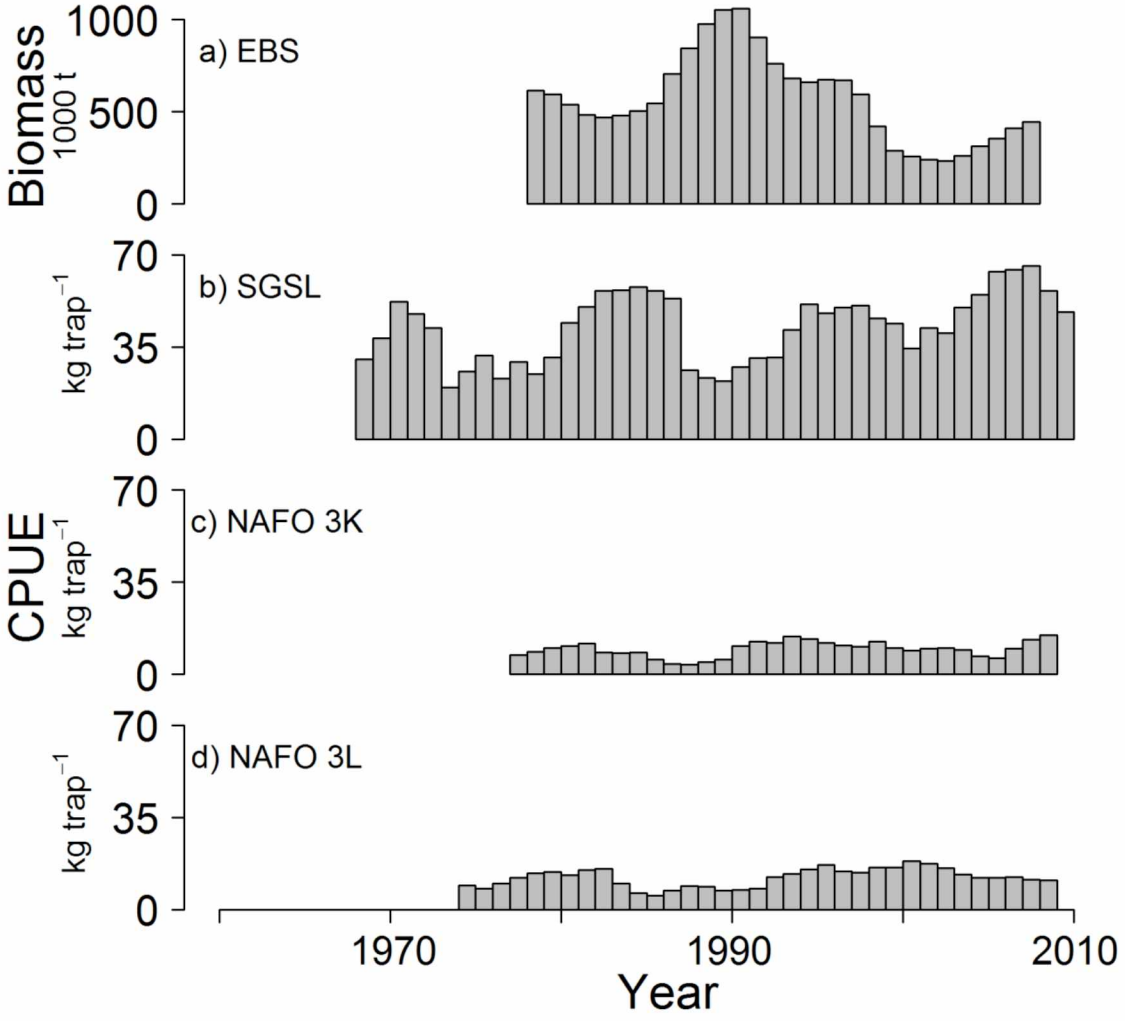

Figure 1.1 Snow crab population trends. Biomass or catch-per-unit-effort of snow crab in four regions. (a) Biomass of snow crab in the eastern Bering Sea. Catch-per-unit-effort of snow crab in (b) southern Gulf of St. Lawrence and Northwest Atlantic Fisheries Organization Divisions (c) 3K and (d) 3L.

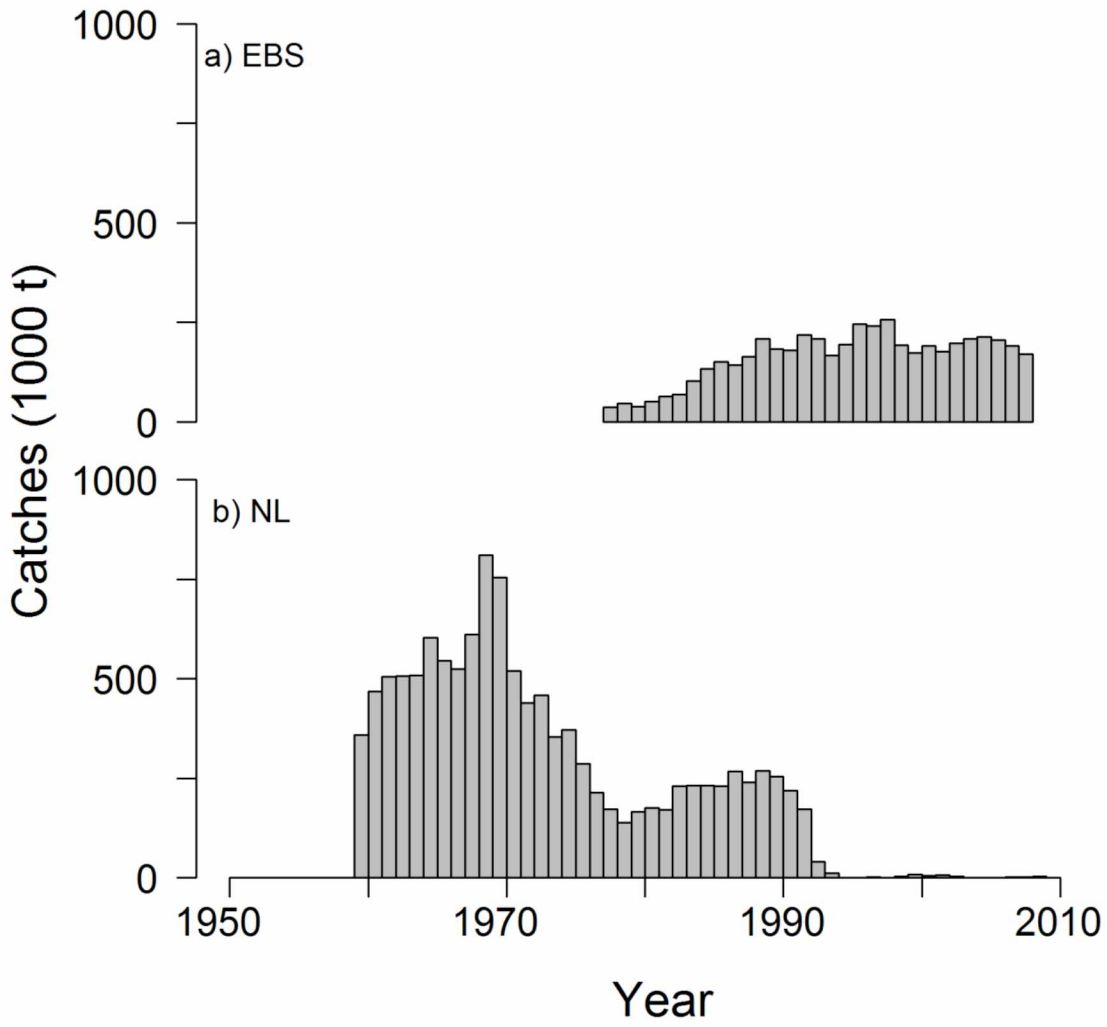

Figure 1.2 Catches of Pacific and Atlantic cod (1000 t). Catches of Pacific cod (*Gadus macrocephalus*) in (a) the eastern Bering Sea (EBS) and total catches of Atlantic cod (*Gadus morhua*) in (b) the Newfoundland-Labrador Shelf (NL) Northwest Atlantic Fisheries Organization Divisions 2J3KL.

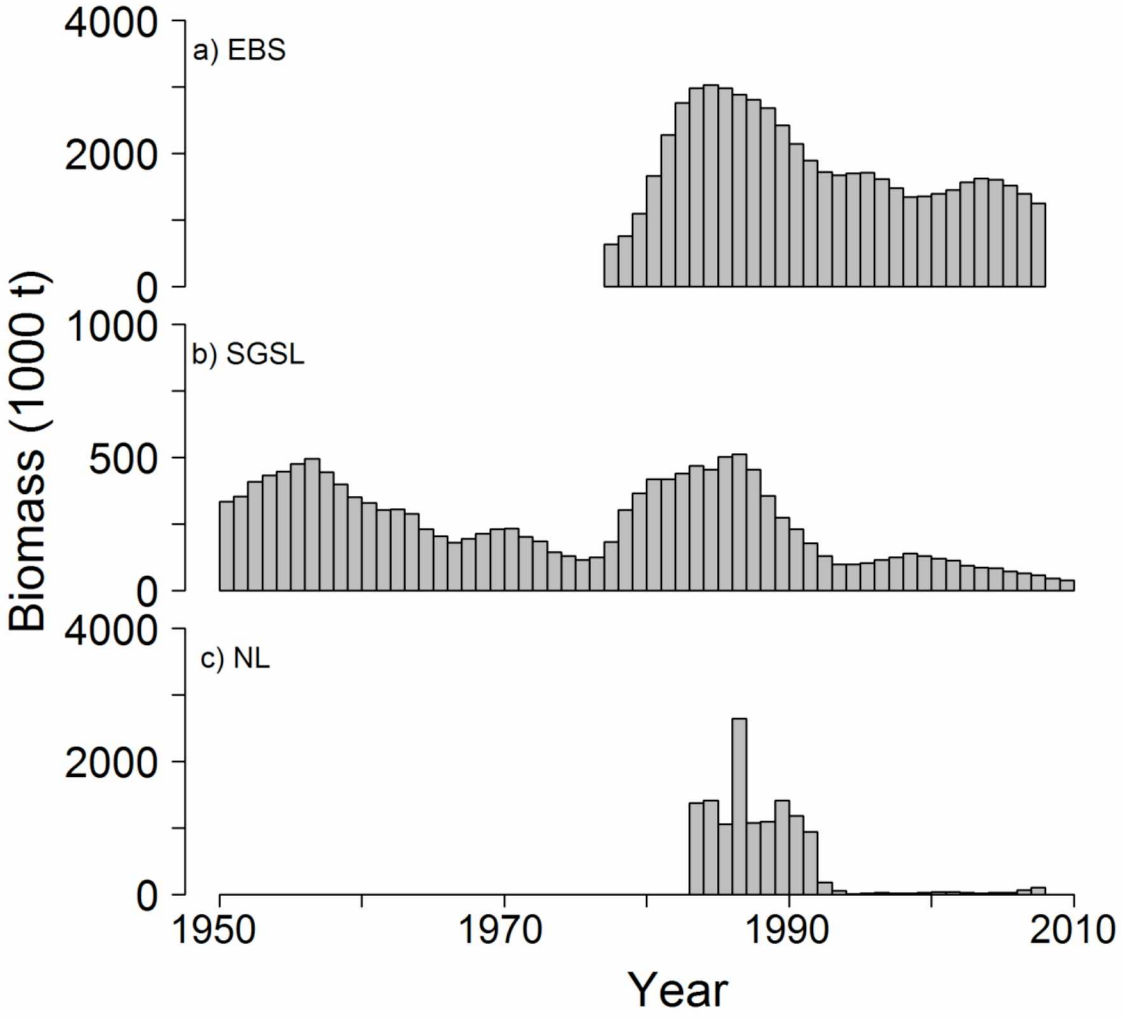

Figure 1.3 Biomass of Pacific and Atlantic cod (1000 t). Biomass of Pacific and Atlantic cod in three regions. (a) Pacific cod (*Gadus macrocephalus*) in the eastern Bering Sea (EBS), (b) Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence and (c) Atlantic cod in the Newfoundland-Labrador Shelf (NL) represented by Northwest Atlantic Fisheries Organization Divisions 2J3KL. Note that the y-axis differs among panels.

Chapter 2: Effects of temperature and gadid predation on snow crab recruitment: Comparisons between the Bering Sea and Atlantic Canada[1]

Abstract

Snow crab (*Chionoecetes opilio*) are found in many subarctic ecosystems where they are important components of marine food webs and support large commercial fisheries. Snow crab abundance is highly variable, but the causes of large changes in year-class strength are poorly known. We used a regression approach to examine the effects of snow crab spawning stock biomass, bottom water temperature, cold area or sea ice extent, and predation by Pacific cod (*Gadus macrocephalus*) or Atlantic cod (*Gadus morhua*) on snow crab recruitment in each of three ecosystems: the eastern Bering Sea, the Newfoundland-Labrador Shelf, and the southern Gulf of St. Lawrence. Comparing results across systems showed that cold ocean conditions during early life history were associated with increased snow crab recruitment or recruitment indices in all three ecosystems. However, we found no consistent evidence that spawning stock or gadid biomasses were significantly related to subsequent recruitment. Our results underscore the value of comparing multiple ecosystems and demonstrate the importance of ocean conditions in driving variability in snow crab populations.

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[1]Marcello LA, Mueter FJ, Dawe EG, Moriyasu M. Effects of temperature and gadid predation on snow crab recruitment: Comparisons between the Bering Sea and Atlantic Canada. Submitted to Marine Ecology Progress Series

2.1 Introduction

Snow crab (*Chionoecetes opilio*) are found in shelf and slope areas of several subarctic ecosystems in the Pacific and Atlantic Oceans (Sainte-Marie et al. 2008). They serve an important trophic role in these systems and support large male-only commercial fisheries. Rational management of these important resources requires a sound understanding of factors that affect their population dynamics.

Snow crab abundance can be highly variable and is believed to be driven largely by changes in the strength of incoming year classes (Zheng & Kruse 2006). However, the drivers of fluctuations in production and survival of these early life history stages, before snow crab are first surveyed, are poorly known. Spawning stock biomass may influence production levels (Zheng & Kruse 2003, 2006) while cannibalism on newly settled juveniles by previously settled year classes may influence survival and contribute to cyclical recruitment (Sainte-Marie et al. 1996, Sainte-Marie & Lafrance 2002). Bottom-up effects from ocean-climate variability may help regulate recruitment and abundance in snow crab (Zheng & Kruse 2006, Dawe et al. 2008, Boudreau et al. 2011). Snow crab generally inhabit regions of very cold water (Sainte-Marie et al. 2008), especially during early benthic and juvenile stages (Dawe & Colbourne 2002, Orensanz et al. 2004), and are energetically confined to cold areas (Foyle et al. 1989). Hence, their distribution and abundance, as well as survival, may be limited by the spatial extent of cold bottom waters. Alternatively, snow crab population dynamics and subarctic ecosystem structure may also be regulated by predation pressure at high trophic levels ('top-down' effects) (Frank et al. 2005, Link et al. 2009). In particular, recent increases

in snow crab biomass in Atlantic Canada may be due to declines in biomass of groundfish predators (Frank et al. 2005). Changes in snow crab recruitment may be influenced by the above factors or others such as disease (Morado et al. 2010, Mullowney et al. 2011) and competition.

By comparing snow crab dynamics across similar ecosystems we may be able to gain a better understanding of what drives ecosystem processes (Murawski et al. 2010). Subarctic ecosystems in both the North Pacific and North Atlantic Oceans share many commonalities including the presence of commercially important snow crab and large gadid predators. This study compares population dynamics of snow crab in the eastern Bering Sea (EBS), the southern Gulf of St. Lawrence (SGSL), and two regions in the Newfoundland-Labrador Shelf (NL) ecosystem to address the following question: Is snow crab abundance governed by common principles across subarctic ecosystems or do snow crab in each ecosystem respond to important drivers in different ways?

Specifically, we investigate how the spawning stock biomass, the environment (water temperature or cold area extent), and the biomass of gadoid fishes impact snow crab recruitment or recruitment indices. Three hypotheses were tested for each of three ecosystems: H_{A1}) snow crab recruitment shows an increasing or compensatory (e.g. asymptotic or dome-shaped) response to spawning stock biomass (density dependence); H_{A2}) colder conditions, represented by lower temperatures, a larger spatial extent of cold bottom temperatures, or more extensive ice cover will result in increased recruitment; and H_{A3}) increased biomass of potential predators will be associated with decreased snow crab recruitment. These hypotheses were tested in a statistical modeling framework

relating estimates or indices of snow crab recruitment to variability in predation, spawning stock biomass, and the environment.

2.2 Methods

2.2.1 Study areas

We examined snow crab dynamics in three subarctic ecosystems that are characterized by a high degree of seasonality in ice cover and sunlight and by large influxes of freshwater (Hunt & Drinkwater 2007). Snow crab generally inhabit shelf or slope areas and are typically associated with a cold pool of water (Sainte-Marie et al. 2008). Relationships between snow crab recruitment or recruitment indices and potential explanatory variables were modeled for four regions in three large marine ecosystems: (1) EBS, (2) SGSL, Northwest Atlantic Fisheries Organization (NAFO) Division 4T, and two regions in NL, (3) NAFO Division 3K (NAFO 3K) and (4) NAFO Division 3L (NAFO 3L) (Fig. 2.1). We chose to model the two NL regions separately, though the crab may be from a single population. Survey data are aggregated at the division level before being combined for the NL system as a whole (DFO 2010); area NAFO 3K corresponds to the Newfoundland Shelf while NAFO 3L is over the Grand Bank.

2.2.2 Data

2.2.2.1 Snow crab data

For the EBS and SGSL time series of estimated recruitment were used as the primary response variable. Hereafter, we use the general term "recruitment" to refer to the estimated or modeled abundance of a specific size-class, which is smaller than the smallest age group recruiting to the fishery. For the EBS, recruits become vulnerable to survey gear over the 30 to 60 mm size range (Orensanz et al. 2004). We used the number of individuals, in millions, between 25 and 40 mm carapace width for the years 1984-2007 as estimated from a statistical, size-structured model based on survey and fishery data (Turnock & Rugolo 2010), and though some crab may be north of the survey area this represents the best available index of recruitment. Recruits to this size class are thought to be 4 years from hatching and 5 years from fertilization (Turnock & Rugolo 2010). Recruitment of instar VIII snow crab in the SGSL was modeled based on survey data from 1989 to 2009 (DFO 2010) and indexed on a scale from 0 to 100 for this study. The SGSL trawl survey was conducted during fall in fishing area 12, which is the largest fishing area in the SGSL. No survey was conducted in 1996 and a model-derived value was substituted for this year (Hébert et al. 1997). SGSL instar VIII snow crab are 30.7 to 34.5 mm carapace width and have been estimated to be 4.3 to 5 years from hatching (Sainte-Marie et al. 1995, Hébert et al. 2002) and though the SGSL recruits cover a narrower size range than in the EBS, the two size classes approximate the same age

range. Snow crab can reach sexual maturity over several different instars, beginning from 35 (Ernst et al. 2005) to 40 mm carapace width (Hébert et al. 2002).

For the two NL regions, available survey time series were too short for modeling purposes. However, fluctuations in the exploitable biomass and abundance are largely dependent on the strength of incoming recruitment to the fishery (males larger than 94 mm carapace width) and should reflect recruitment of the youngest year classes entering the fishery (approximately age 10). Therefore, we used variability in catch-per-unit-effort (CPUE in kg $trap^{-1}$ for snow crab > 94 mm carapace width) as a recruitment index recruitment in these regions (1977-2008 for NAFO 3K, 1974-2008 for NAFO 3L). Hereafter, we refer to these CPUE series as "recruitment index."

The reproductive potential of snow crab should influence larval production and this may be reflected in variations in recruitment. To address our first hypothesis linking spawner biomass to later recruitment, we used proxies for spawning stock biomass as measures of reproductive potential. In the EBS we used an estimate of total mature snow crab biomass (males and females) from the 2007 stock assessment. In all other areas (SGSL, NAFO 3K and 3L), CPUE of male snow crab 95 mm carapace width or larger was used as a proxy for spawning stock biomass, hereafter called "spawning stock biomass index". These measures were incorporated at appropriate lags in regression models to assess potential impacts of spawner biomass on recruitment as described below.

2.2.2.2 Environmental data

To capture the potential effects of ocean climate variability on snow crab recruitment we selected bottom temperatures and cold area extent (measured either as the extent of the cold layer of water that forms as a result of winter ice cover or as the spatial extent of the sea ice itself) as environmental variables for modeling.

For the EBS, a long-term proxy for bottom temperature was constructed using the NOAA extended reconstructed sea surface temperature data series (Smith et al. 2008, NOAA 2011). The proxy uses sea surface temperatures averaged over the spring and late summer periods (March, April, May, and August) when water column temperatures were most strongly correlated with average bottom temperatures over the shelf (Pearson's product moment correlation $r = 0.88$) due to vertical mixing. Bottom temperatures in the SGSL were measured annually at Magdalen Shallows during September (Chassé & Pettipas 2010). For both NL areas (NAFO 3K and NAFO 3L) a time series of annual mean bottom temperatures at Station 27, an oceanographic monitoring station located 7 km from St. John's Harbour (Newfoundland), was selected as a measure of temperature variability in these regions (Dawe et al. 2008).

Seasonal ice cover is an important feature of all the study areas examined here. It determines the spatial extent of the cold pool in the EBS and is related to the area of the cold intermediate layer in Atlantic Canada. Because the spatial extent of these cold waters has important effects on the distribution of snow crab (Dionne et al. 2003, Orensanz et al. 2004), we examined the influence of cold area extent in each region. For the EBS, cold area extent represents the fraction of the National Marine Fisheries Service

summer bottom trawl survey area with water less than 2°C (F. Mueter, unpubl. data). The SGSL cold area variable represents the area (km^2) of Magdalen Shallows covered by -1 to 3°C bottom water during September (Chassé & Pettipas 2010). For NAFO 3K and NAFO 3L the annual ice cover area (km^2) from 45-55°N on the Newfoundland-Labrador Shelf (Dawe et al. 2008) was used to represent the spatial extent of cold water.

2.2.2.3 Predators

To examine the potential effects of key predators on snow crab recruitment in each system, and to address hypothesis H_{A3}, suitable estimates of predator biomass were compiled. Although there are many predators of snow crab, this study focused on predation by gadoid fishes. Walleye pollock (*Theragra chalcogramma*) dominate gadid biomass in the EBS, but were not included here because snow crab make up a very small proportion of their diet (Aydin et al. 2007). The major gadid predator on snow crab in the EBS is Pacific cod (*Gadus macrocephalus*) (Livingston 1989) and we used a model-based estimate of the total biomass of Pacific cod age 0+ from the 2007 stock assessment model (Thompson et al. 2010) to quantify potential gadid predation in this system. In both Atlantic Ocean ecosystems, Atlantic cod (*Gadus morhua*) has historically been a major predator of snow crab. In the SGSL, Atlantic cod age 3+ biomass estimates from the 2009 stock assessment model (Swain et al. 2009) were used to examine predation effects. In NL regions NAFO 3K and 3L, estimates of total Atlantic cod biomass from autumn surveys (conducted through 2007) were used.

2.2.3 Analytical approach

A general regression approach was used to examine the effects of snow crab spawning stock biomass, environmental variability, and predation on snow crab recruitment in each ecosystem. The basic modeling structure was as follows:

$$y_t = \beta_0 + \beta_1 \text{ spawners}_{t-k1} + \beta_2 \text{ environment}_{t-k2} + \beta_3 \text{ predator}_{t-k3} + \varepsilon_t \quad (1)$$

where y_t represents snow crab recruitment (or recruitment index) in year t, βs are regression coefficients, $k1$, $k2$, and $k3$ represent time lags, and the errors ε_t are assumed to be either independent and normally distributed with mean zero and variance σ^2 or first-order autocorrelated ($\varepsilon_t = \phi\, \varepsilon_{t-1} + \nu_t$) with auto-regressive coefficient ϕ and innovations ν_t that are independent and normally distributed.

Recruitment data often have a skewed distribution and may require a transformation to achieve normality in model residuals. A range of Box-Cox transformations (Box & Cox 1964) were explored to identify the best power transformation for each response variable (y_t) to achieve approximate normality of the residuals. Likelihood profiles indicated that a log transformation was the best possible transformation for the EBS and SGSL recruitment series, while no transformation was necessary for the NAFO 3K and NAFO 3L recruitment indices.

Spawning stock biomass affects larval production, while both predation and the environment may influence survival to recruitment. Each of these factors would be expected to alter population abundances several years prior to recruitment and the effects may extend over multiple years, necessitating the use of lags and moving averages for the explanatory variables. Available diet studies suggest that early life history stages of snow

crab are particularly vulnerable to predation (Livingston 1989, Chabot et al. 2008). For example, in the Gulf of St. Lawrence four size groups of crab were susceptible to Atlantic cod predation (Chabot et al. 2008). These sizes roughly correspond to ages 1 to 4 (Hébert et al. 2002) although there can be some variability in growth to each size class. Similarly, environmental conditions including temperature can affect larval and juvenile stages of snow crab by influencing development rate (Moriyasu & Lanteigne 1998), hatch timing (Webb et al. 2007), growth rate, and molt frequency (Orensanz et al. 2007), as well as energy budgets (Foyle et al. 1989). Since effects may range over several life stages and because snow crab cannot be aged reliably, 3 or 4-year moving averages were applied to time series of both predators and environmental variables to capture their potential effects on multiple age classes of snow crab. Likewise, moving averages were applied to spawning stock biomass series because the time period between fertilization and growth to the recruitment size class varies. The averaged variables were then lagged by k years relative to the response in year t to correspond to the approximate period when the effect is presumed to occur (year t-k). For example, the recruitment of EBS snow crab is most likely to be influenced by the parental stock 4-6 years prior (Table 2.1), hence recruits measured in 1995 were modeled as a function of the spawning stock biomass averaged over 1989 to 1991. In some cases, several biologically reasonable lags were considered such as in NL regions NAFO 3K and NAFO 3L where snow crab were measured after reaching commercial size. In those areas it was reasonable to consider predation effects over several lags (ranging from 5-8 years to 7-10 years prior) due to uncertainty and variability in the age at which snow crab reach commercial size. When

multiple lags were considered, the lag that resulted in the lowest p-value in a simple linear regression between the recruitment index or log of recruits and each explanatory variable was selected for use in regression models. The lags and averages used for all variables in each model are listed in Table 2.1.

For some ecosystems the length of overlapping time series was limited once the predator and/or spawner series were lagged appropriately. For these systems both "short models" including all variables and "long" models including fewer variables were tested. For example, the Atlantic cod series in NAFO 3L overlapped with the response variable by only 16 years, whereas the spawner and environmental variables were available over longer time periods (n = 24 and n = 35 years, respectively). Results from analyses using the short and long series were then compared for consistency. We considered the results to be consistent when the sign of all explanatory variables remained unchanged regardless of whether the short or the long series were used.

A species may exhibit non-linear, non-additive, or threshold responses to external pressures (Cury et al. 1995, Ciannelli et al. 2007, Ciannelli et al. 2008). To explore potential non-linearities and thresholds we fit exploratory generalized additive models (GAMs) to the data using a cross-validation approach before constructing a corresponding linear model for further analysis. To avoid over-fitting we limited parameter smoothness by constraining the estimated degrees of freedom (EDF) for any variable to 3, corresponding to a biologically realistic set of possible responses (approximately linear, asymptotic, or dome-shaped). Partial fits for each explanatory variable and the estimated degrees of freedom were examined and a squared term was

included in the full linear model for any variable with EDF > 1.5. No higher-order polynomial terms were considered as they were not deemed biologically reasonable.

For each ecosystem both a temperature variable and cold area extent (or sea ice extent) were available for modeling. However, bottom temperatures were strongly correlated with cold area cover and/or sea ice extent in each system (multicollinearity). Therefore, the effects of these variables were modeled separately and compared for consistency. For each system, the initial full linear model included one environmental variable, a cod predator, and spawning stock biomass. We tested for interactions among variables in each full model, and because we found no significant interactions, we did not consider interactions further. We compared the full model with all three variables to reduced models with one or two variables using the small-sample Akaike Information Criterion (AICc). The model with the smallest AICc was selected as the final model when the difference between AIC values, ΔAICc, was larger than 4 (Burnham & Anderson 2002). If differences in AICc were smaller than 4, the most parsimonious model was selected as the final model.

Residuals from both the initial (full) model and from the final (AICc-best) model were examined for normality, heteroscedasticity, and autocorrelation. When significant autocorrelation ($p < 0.05$) was present in residuals from the full model according to a Durbin-Watson (DW) test, all model comparisons were based on generalized least squares fits that included a first-order auto-regressive error term. The overall significance of the final (AICc-best) model was tested using the likelihood ratio test

(LRT) for generalized least squares models or F-test for linear models without autocorrelation.

Program R version 2.9 (R Development Core Team 2011) was used for all analyses and a level of $\alpha = 0.05$ was chosen to assess significance.

2.3 Results

In the EBS cold temperatures were related to increased recruitment, consistent with our hypothesis, but results did not support a predation effect (Tables 2, 3). The final model included temperature and spawning stock biomass; both variables were negatively and linearly related to the log of recruitment ($n = 24$ years, $LRT = 20.75$, $p < 0.001$) and explained approximately 38% of the variability in recruitment (Fig. 2.2a). The model included a first-order auto-regressive term ($\varphi = 0.66$) to account for significant autocorrelation in the residuals ($DW = 0.93$, $p < 0.001$, Fig. 2.3a). When replacing temperature with the cold area extent ($n = 22$ years) in the full model, its estimated effect was not significant ($t = 1.45$, $p = 0.164$), but its sign was consistent with a positive effect of cold conditions on recruitment.

In the SGSL we found a negative linear relationship between temperature and the log of recruitment, but neither a predation nor a spawner effect ($n = 21$ years, Tables 2, 3). The final model included the temperature variable ($LRT = 20.81$, $p < 0.001$, Table 2.2) and explained about 41% of the recruitment variability (Fig. 2b). A first-order auto-regressive term ($\varphi = 0.73$) was included in the model to account for residual autocorrelation ($DW = 0.77$, $p < 0.001$, Fig. 2.3b). The full model for SGSL based on

cold area extent rather than temperature was not significant overall (LRT = 4.66, p = 0.32) and contained no significant variables ($p > 0.05$). Therefore, models with cold area extent were dropped from further consideration.

In NL area NAFO 3K sea ice extent was positively related to the snow crab recruitment index 7-9 years later (Table 2.2) corresponding approximately to the time a crab entering the fishery would have been 1-3 years of age. There was no evidence of an effect of spawner stock biomass index or temperature on snow crab recruitment index and the estimated effects of Atlantic cod were inconsistent (Table 2.3). Models for NAFO 3K that included the Atlantic cod series (n = 18 years) differed substantially from those including just other variables (n = 21 for spawners, n = 32 for temperature or ice area). Specifically, when Atlantic cod biomass was included in these models, the sign and significance of other coefficients changed drastically, most likely as a result of strong correlations between Atlantic cod and the other explanatory variables. Therefore, models including Atlantic cod were not considered further. Spawner stock biomass index was neither significant to the model with bottom temperature nor to the model using sea ice extent as a proxy for the cold area extent. Sea ice extent had a significant positive linear relationship with the snow crab recruitment index (Table 2.2), though it only explained a small proportion of overall variability (Fig. 2.2c, n =32 years, LRT = 33.00, $p < 0.001$, $R^2 = 0.18$). A first-order autoregressive term ($\varphi = 0.91$) was included to account for significant autocorrelation in the residuals (Fig. 2.3c, DW = 0.45, $p < 0.001$). When using bottom temperature as the environmental variable, none of the variables in the model

were significant ($p > 0.05$), but a negative temperature coefficient was consistent with the observed positive effect of extensive ice on the snow crab recruitment index.

In the other NL region, NAFO 3L, cold conditions and low predator biomasses were associated with a high recruitment index in following years. Spawner stock biomass index showed a negative association with later the recruitment index (Tables 2, 3). Models including Atlantic cod covered a shorter time period (n = 16 years) than those with spawner stock biomass index (n = 24 years) or environmental conditions (temperature or sea ice extent, n = 35), but the sign of coefficients for spawner stock biomass index and temperature or sea ice extent remained consistent among models. Temperature or sea ice extent were significant in all models, though spawner stock biomass index was not significant in the longer (n = 24 years) model. In the short models spawner and predator biomasses were both negatively related to the subsequent snow recruitment index. Likewise, colder conditions were linked with a higher recruitment index. Both model fits explained about 90% of recruitment index variability over the 16 years modeled (temperature model: $F_{(3,12)} = 45.62$, $p < 0.001$; sea ice extent model: Fig. 2.2d, $F_{(3,12)} = 43.91$, $p < 0.001$) and there was no evidence of first-order autocorrelation in the residuals (temperature model: DW = 2.05, p = 0.22; sea ice-extent model: Fig. 2.3d. DW = 2.04, p = 0.22).

Significant and pronounced autocorrelation was present in the recruitment or recruitment index residuals in the final models for three of four regions studied (EBS, SGSL, and NAFO 3K in the NL ecosystem), as was clearly evident in residual plots (Fig. 2.3). The first-order autoregressive structure of the generalized least squares models

accounted for the observed serial correlation and ensured that significance tests and model comparisons are valid. However, clear cyclic patterns with several multi-year runs of alternating positive and negative residuals were evident in both the full models and in the AICc-best models. This suggests that models including environmental variables, predation and/or spawner effects, in combination with random measurement errors, do not fully account for the dynamics of these populations.

2.4 Discussion

2.4.1 Overview

This study investigated the effects of three factors (spawning stock biomass, environmental conditions, and gadid biomass) on the strength of subsequent recruitment levels in snow crab and compared results across three subarctic ecosystems in the Northwest Atlantic and Northeast Pacific (Table 2.3). Our modeling results showed that ocean climate variability was the only factor that was consistently associated with recruitment in all ecosystems and regions. This strongly supports our hypothesis (H_{A2}) that cold conditions during early life history stages promotes subsequent snow crab recruitment (Fig. 2.4). In contrast, there was little support for a consistent effect of spawning stock or predator biomasses (hypotheses H_{A1} or H_{A3}) on recruitment across systems. Spawning stock biomass had an apparent negative impact on recruitment in the EBS and NAFO 3L, possibly indicating a density-dependent effect on recruitment in

those areas. Atlantic cod biomass had an apparent negative impact on recruitment, consistent with predation, but only in NAFO 3L.

Our study shows that bottom-up processes related to ocean climate conditions appear to have a consistent influence on snow crab recruitment while the importance of gadid biomass or spawning stock biomass is less clear. This study also highlights the value in comparing multiple ecosystems because consistent responses across several systems greatly strengthen our conclusions about significant effect of temperature conditions to early life stages of snow crab.

2.4.2 Environment, spawning stock biomass, and predation

Our study suggests that colder conditions during early life are associated with better snow crab recruitment in all of the systems examined. Our indices of ocean climate are closely related, and we did not address mechanisms linking climate to snow crab life history, so it is unclear whether these indices reflect a common regulatory mechanism or if they represent different processes. Climate can be linked to snow crab reproduction and survival in several ways. For example, the hatch timing of larval crab is linked to temperature (Webb et al. 2007) and ice cover can affect stratification and larval feeding conditions in the spring (Orensanz et al. 2004). Recently settled juveniles are thought to be very stenothermic and have low mobility; they could represent the "weakest link" in snow crab life history because they cannot easily escape unfavorable environmental conditions such as unfavorable temperatures (Dionne et al. 2003). Therefore, the area of cold water during summer may limit the amount of suitable habitat

and hence the carrying capacity for early benthic stages (Dawe & Colbourne 2002). In addition, temperature likely affects early survival directly by regulating the energy budget of individual crabs (Foyle et al. 1989). A laboratory experiment found that for mature male snow crab taken from the Scotian Shelf, their total metabolic costs exceeded digestible energy in waters 7°C or higher and slightly exceeded digestible energy in 0-1 °C water (Foyle et al. 1989). Therefore, snow crab may be excluded from warm waters based on energetic demands (Foyle et al. 1989). Conversely, it is known that cold conditions promote snow crab to terminally molt at a smaller size, which may reduce the proportion of commercially harvestable males in the total adult male population (Dawe et al. submitted for publication-b). Overall, the effects of temperature or cold area extent on early life stages seem to have a dominant effect on recruitment. However, in this study mean temperatures in each system varied within a narrow range (roughly 1.5°C) and so recruitment responses should not be extrapolated outside of the modeled temperature range. The relationships to temperature we found differ among ecosystems, which is likely due to each stock being adapted to a local temperature regime. Therefore, the effect of a given temperature on recruitment must be related to typical conditions for that stock.

For the cod predators considered in this study, we found a significant effect on recruitment only in NAFO 3L in the NL ecosystem. Considering the absence of any such effect in other regions, especially in the adjacent NAFO 3K area, our study found little evidence that cod biomass exhibited top-down control on larval and juvenile snow crab since the late 1970s. In both the Newfoundland-Labrador Shelf (Lilly 2008) and in the

Gulf of St. Lawrence (Ruppert et al. 2010), Atlantic cod populations have crashed from their historic levels and were at low abundances during most of the time period examined here. Consequently, there simply may be too few cod at the present time to exert significant population-level predation effects on young snow crab. The apparent predation effect in NAFO 3L may also result from opposing responses of snow crab and Atlantic cod to ocean climate variability, with snow crab increasing and cod decreasing during a prolonged cold period when cod was also excessively exploited (Dawe et al. 2008). However, our results do not imply that predation has no effect on snow crab recruitment. Previous studies indicate that predation may be important. For example, Livingston (1989) estimated that in the EBS, Pacific cod remove 27-57 percent of age 1 snow crab from the population. Our results may differ for several reasons. First, the spatial scale of data may influence statistical analyses (Ciannelli et al. 2008) and hence our results. Biological data for this study represented large geographic regions and will fail to detect small-scale predator-prey interactions. Second, predation can have indirect effects on snow crab recruitment by limiting their geographic range. Climate conditions may affect predator-prey relationships by altering the spatial distributions of either species (Zheng & Kruse 2006). Also, the EBS snow crab population has contracted northward in recent decades (Orensanz et al. 2004). The environmental ratchet hypothesis proposes that Pacific cod predation may help prevent snow crab from expanding and returning to more southern portions of the eastern Bering Sea shelf that provide favorable spawning habitat (Orensanz et al. 2004). Such spatial dynamics can lead to important predation effects that may not be evident in a relationship between time

series of aggregated predator biomasses and recruitment. Finally, the diet of both cod species changes with age (Livingston 1989, Chabot et al. 2008) and the age classes of cod which are the most important consumers of snow crab may not be well-represented in aggregated biomass series.

A recent meta-analysis by Boudreau et al. (2011) looked for evidence of top-down and bottom-up controls on snow crab in the northwest Atlantic Ocean. Similar to our study, their results linked colder temperatures with higher snow crab abundance during the early years after settlement. Conversely, they found statistical evidence of top-down control by Atlantic cod on snow crab 0 to 5 years later. For crab entering the fishery these lags would correspond to snow crab approximately 29 - 97 mm carapace width or 3.3 – 8.7 years of age. Their result was somewhat unexpected because cod generally do not consume hard-shell snow crab that are 4.5 years post-settlement or older (Chabot et al. 2008) and predation by cod on crabs in the northwest Atlantic has been virtually non-existent throughout during the time period used, due to very low abundance of large-bodied cod (Dawe et al. submitted for publication-a). However, at the longer lags, which correspond to younger crab, their results may conform to expectations from available diet studies. Our predation results may differ from those found in Boudreau et al. (2011) in part due to methodological approaches. We made an *a priori* assumption about the crab ages most vulnerable to predation to choose lags attempting to minimize the chance of finding spurious relationships. Boudreau et al. (2011) considered a much larger range of lags (25 years) since they were examining both the effects of crab on cod and of cod on crab. We used a regression approach that allowed us to consider multiple

covariates at once whereas they considered full and partial correlation coefficients focusing on each relationship independently.

The lack of a relationship we observed between cod biomass and snow crab recruitment may reflect a true absence of top-down control by cod on snow crab. However, in light of the results from Boudreau et al. (2011) and the aforementioned drawbacks of using biomass as an indicator of overall predation pressure, we cannot discount top-down controls of cod on snow crab.

Spawning stock biomass did not show a consistently positive or dome-shaped relationship with recruitment, as we hypothesized. Rather, it was significantly negatively correlated to subsequent recruitment in two areas (EBS, NAFO 3L in the NL ecosystem). This relationship could occur if our data represented the right (declining) limb of a dome-shaped curve, however, that would mean that the spawn-recruit relationships peak at low spawner biomasses. Also, numerous factors may affect the survival of young crab in the years between fertilization and when recruits are first measured. Cannibalism may reduce the abundance of recently settled snow crab (Sainte-Marie & Lafrance 2002) and could perhaps confound or even mimic spawning stock biomass effects, particularly in the EBS and SGSL regions where the lag time between spawners and recruits was relatively short. In addition, several elements of snow crab reproductive biology may mask any direct link between adult spawning stock biomass and later recruitment. Female snow crab are able to store sperm and to use these reserves to fertilize ova (Elner & Beninger 1992), so current male or total biomass may not reflect reproductive potential in a given year. In addition, the length of embryo development (Webb et al. 2007) and

the overall reproductive cycle varies and is thought to be influenced by temperature (Kuhn & Choi 2011) and by whether the female is a primiparous or multiparous spawner (Elner & Beninger 1992). A crab that remains on a one year reproductive cycle can produce up to twice as many clutches over its reproductive lifetime than a crab on a two year reproductive cycle (Kuhn & Choi 2011). Therefore, the proportion of crab reproducing on each cycle can have a large impact on a population's overall fecundity. Finally, the geographic distribution of female snow crab may affect reproductive success. For example, in the EBS female snow crab undergo ontogenetic migrations (Ernst et al. 2005). Parada et al. (2010) used an individual-based model in the EBS to show that larval retention, and presumably recruitment success, varies greatly depending on the location of larval release. They also hypothesize that primiparous females, which aggregate in the middle domain of the EBS, may be the largest source of renewal for the EBS snow crab stock (Parada et al. 2010). Hence we may have failed to detect any relationship between measures of spawning biomass and recruits because spawning biomass is weakly related to total reproductive output.

Another important finding from this study is that the variables we modeled cannot fully explain the observed cycles in recruitment that are characteristic of snow crab and other crab populations. This is evident in the residual patterns for three of the regions modeled here (Fig. 2.3) and is likely to result from internal community dynamics. Such dynamics may be linked a stronger contribution of primiparous than multiparous females to recruitment (Parada et al. 2010) or because of cannibalism among cohorts within settlement grounds (Sainte-Marie et al. 1996). Alternatively, small-scale changes in

climate related to atmospheric circulation like the El Niño could be related to snow recruitment cycles (Zheng & Kruse 2003). Residual cycles could also be related to changes in predation pressures owing to the spatial distribution of snow crab or their predators, as discussed earlier.

2.4.3 Implications for stock assessment and management

Reliable stock assessment provides the foundation for successful fisheries management. Stock assessment scientists must make assumptions about recruitment levels to project future snow crab populations, to evaluate the effects of harvesting, and to develop or compare rebuilding plans (NOAA 2001) for depleted stocks. The dominant role of bottom-up climate processes in regulating recruitment and the cyclic patterns we observed in model residuals imply that productivity is not stationary. Incorporating ocean climate effects and population cycles into projections will lead to more reliable predictions of future recruitment that would result in improved management advice. Precautionary reference points, guideline harvest levels, and thresholds for overfishing should be set to reflect variability in production and subsequent recruitment. Further, the current study indicates that warm conditions are linked with poor recruitment. Therefore, if climate change causes bottom conditions to continue to warm, snow crab recruitment will likely decline in our study areas. Studies such as ours, if applied to other important predatory and forage species, can be very important in developing a better basis for ecosystem-based management, especially under a scenario of a changing ocean climate.

2.5 Acknowledgements

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Table 2.1 Explanatory variables and lags used in modeling.

Explanatory variables used in this study by region with lags considered for each variable. Lags denote the time range (in years) prior to the year when recruitment (eastern Bering Sea, EBS; southern Gulf of St. Lawrence, SGSL) or recruitment indices (in Newfoundland-Labrador NAFO Divisions 3K and 3L) was measured. Ranges include only those years during which explanatory variables may reasonably be expected to affect snow crab subsequent recruitment.

Region	Explanatory Variable	Lags (years)
EBS	Spawners	4-6
	Temperature	2-4
	Cold area cover	2-4
	Pacific cod	2-4
SGSL	Spawners	4-6
	Temperature	3-5
	Cold area cover	3-5
	Atlantic cod	2-4
NAFO 3K	Spawners	9-11
	Temperature	7-9
	Sea ice extent	7-9
	Atlantic cod	5-8
NAFO 3L	Spawners	9-11
	Temperature	7-9
	Sea ice extent	7-9
	Atlantic cod	7-10

Table 2.2 Model results with regression coefficients.

Regression coefficients with p-values (in parentheses) for final model fits of snow crab recruitment or fishery recruitment indices in four regions (eastern Bering Sea, EBS; southern Gulf of St. Lawrence, SGSL; NAFO Division 3K, NAFO 3K; and NAFO Division 3L, NAFO 3L). Coefficients denote intercept (β_0) and estimated effects of spawning stock biomass (β_1), temperature or sea ice extent (β_2), predator biomass (β_3), and a first-order autoregressive parameter (φ), if significant. Predators are Pacific cod in the EBS and Atlantic cod elsewhere.

Region	Environmental Variable	β_0	β_1	β_2	β_3	φ
EBS	temperature	16.50	-5.38×10^{-3}	-2.12		0.66
		(<0.001)	(0.032)	(0.006)		
SGSL	temperature	5.12		-2.85		0.73
		(<0.001)		(0.020)		
NAFO 3K	sea ice extent	6.80		4.72		0.91
		(0.035)		(0.034)		
NAFO 3L[a]	temperature	20.27	-0.65	-2.73	-9.63×10^{-3}	
		(<0.001)	(<0.001)	(0.008)	(0.001)	
	sea ice extent	20.91	-0.70	2.98	-9.63×10^{-3}	
		(<0.001)	(<0.001)	(0.011)	(0.001)	

[a] Results based on model fit to 16 years with data for all variables. See text for results from longer model (n=24 years) that did not include Atlantic cod.

Table 2.3 Comparing ecosystems

Summary of estimated effects of spawning stock biomass, the environment, and predation by cod on snow crab recruitment. For the eastern Bering Sea (EBS) and southern Gulf of St. Lawrence (SGSL) the response variable was the log of the estimated number of recruits at a small size. In the two Newfoundland/Labrador systems (NAFO 3K and NAFO 3L) a fishery recruitment index was the response variable. Predators are Pacific cod (EBS) and Atlantic cod (SGSL, NAFO 3K, NAFO 3L).Variables that were significant to the final models are shown in plus or minus signs, while those that are not significant are indicated by NS.

	EBS	SGSL	NAFO 3K	NAFO 3L
Spawners	-	NS	NS	- [a]
Temperature	-	-	NS	-
Cold Area Cover / Sea Ice Extent	NS	NS	+	+
Predators	NS	NS	(b)	-

[a] Spawners were negatively related to CPUE in both short and long models; however they were only significant in the short model. [b] Results from models including and excluding Atlantic cod were not consistent.

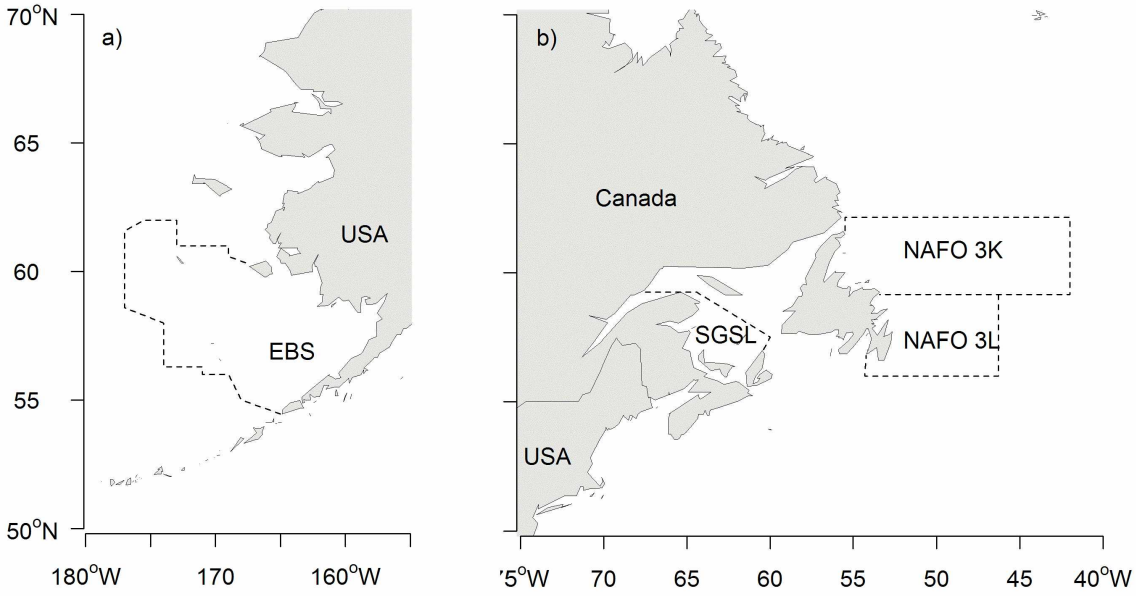

Figure 2.1 Study regions

Study regions used to model the effects of spawners, the environment, and predation by gadoid fishes on snow crab recruitment in (a) the eastern Bering Sea (EBS) and (b) the NAFO Division 4T in the Gulf of St. Lawrence (SGSL), and NAFO Divisions 3K (NAFO 3K) and 3L (NAFO 3L) off the Newfoundland-Labrador Shelf.

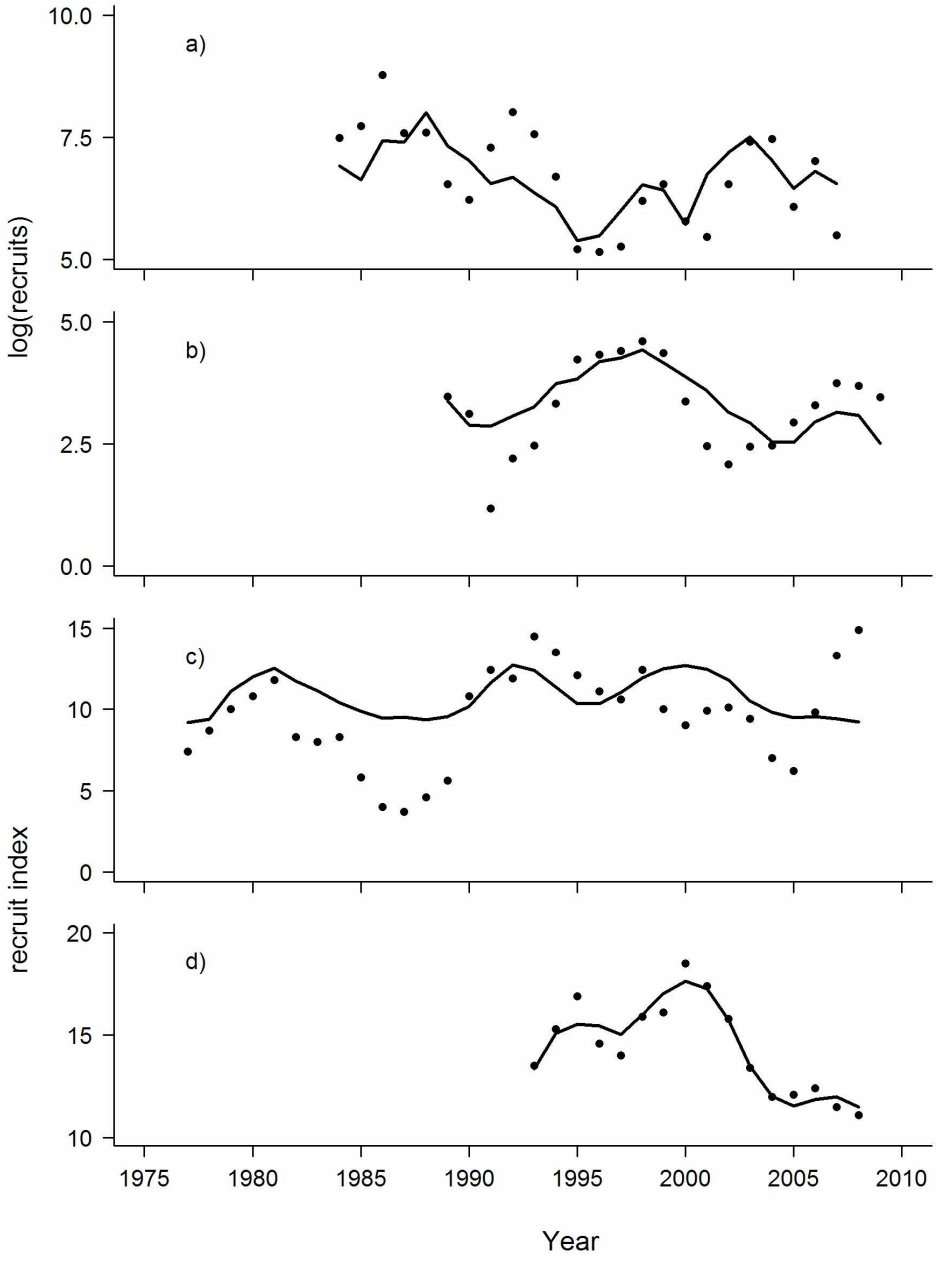

Figure 2.2 Model fits

Time series of snow crab recruitment or recruitment index (dots) with predicted values from best-fit models (lines) for (a) the eastern Bering Sea (b) the southern Gulf of St. Lawrence, (c) NAFO 3K, and (d) NAFO 3L (sea ice extent model). Best-fit models for each region are described in the text and summarized in Table 2.2.

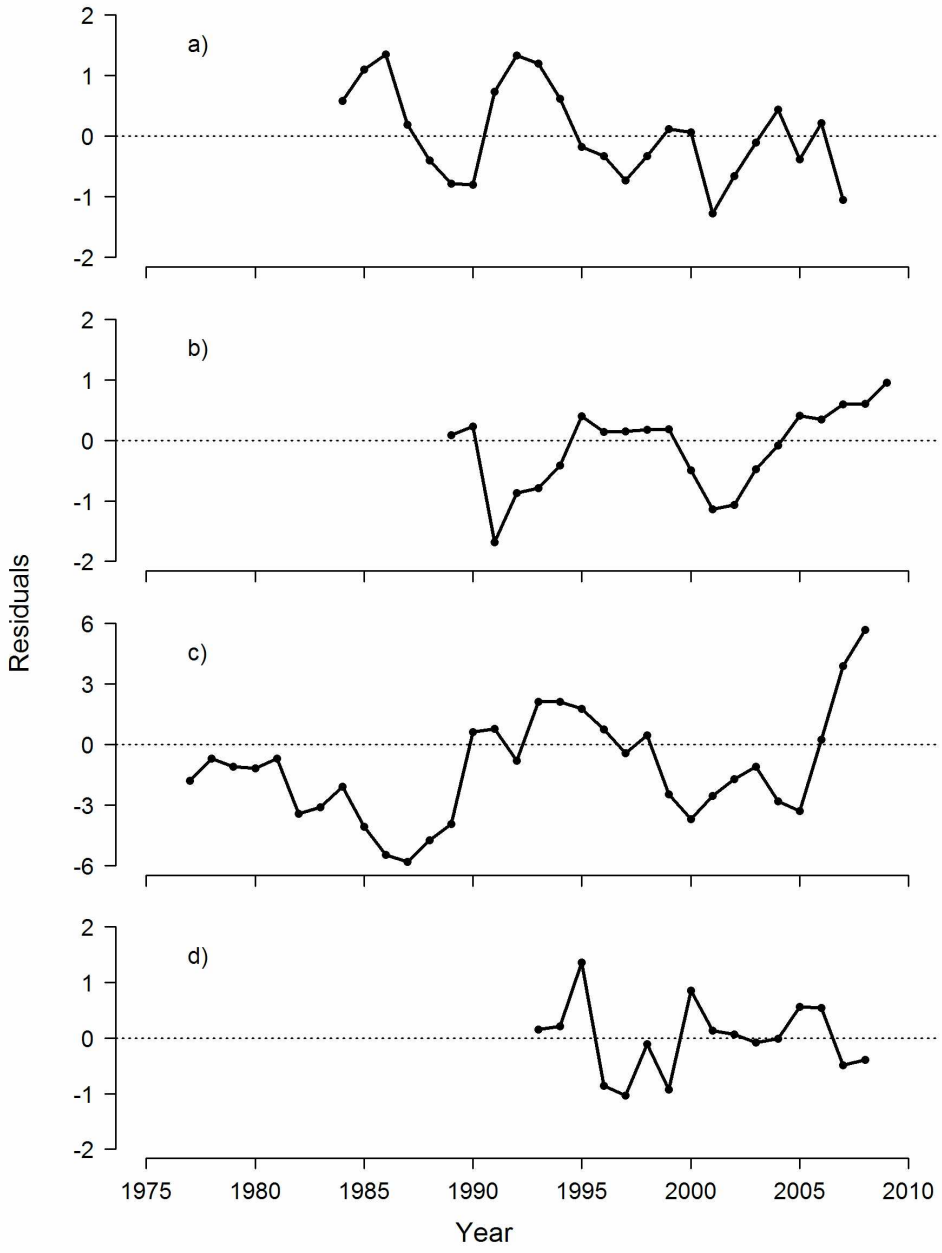

Figure 2.3 Model residuals through time

Model residuals though time for four geographic regions: (a) the eastern Bering Sea, (b) the southern Gulf of St. Lawrence, (c) NAFO 3K, and (d) NAFO 3L (sea ice extent model). Residuals from several models have long runs of negative and positive residuals indicating a possible cyclical pattern in recruitment.

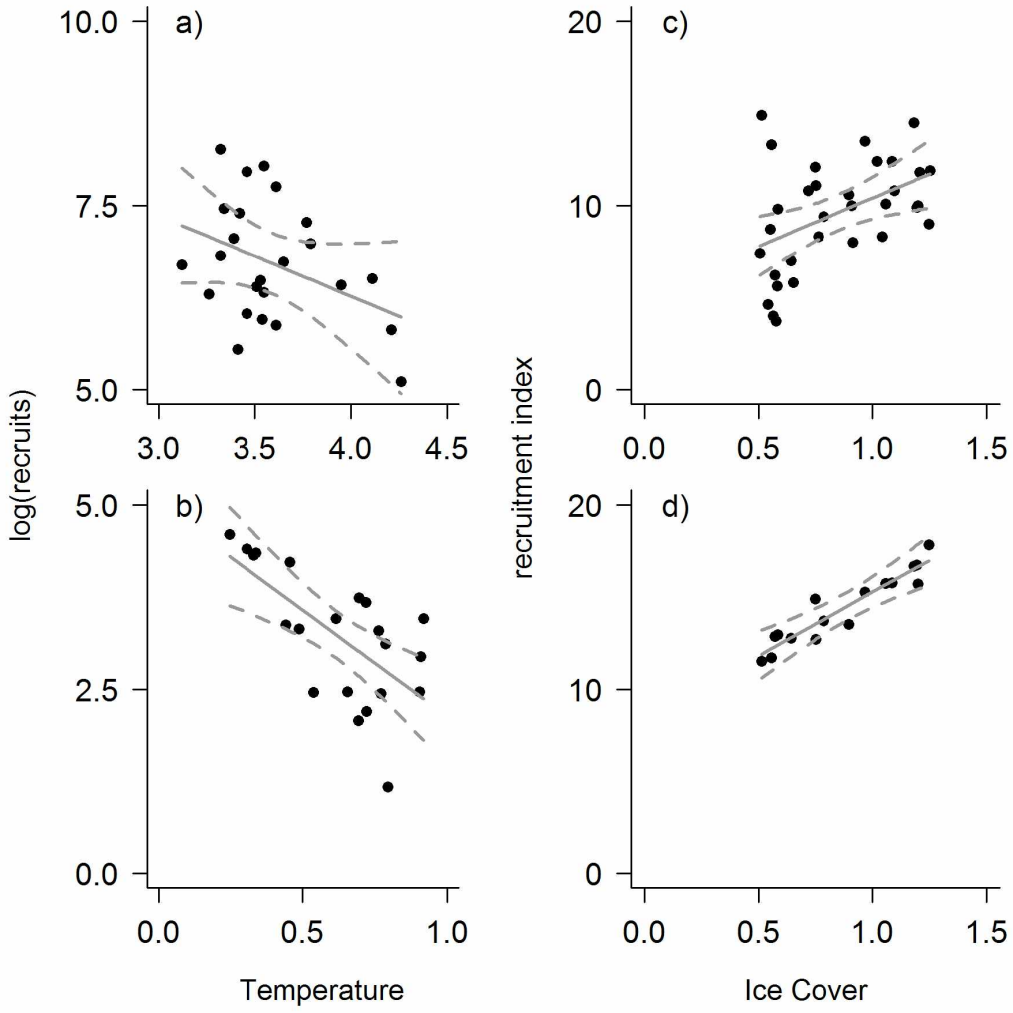

Figure 2.4 Relationship between climate and snow crab recruitment.

Partial fits (solid lines) with 95% pointwise confidence intervals (dashed lines) illustrating the estimated effects of temperature and ice conditions on recruitment, while holding other variables constant at their mean values. Plots show the effect of temperature on recruitment in (a) the eastern Bering Sea and (b) southern Gulf of St. Lawrence and the effect of ice cover on recruitment indices in (c) NAFO Division 3K and (d) NAFO Division 3L. Note that the axes differ among panels.

General Conclusions

The overall goal of this project was to examine the drivers of snow crab population dynamics in subarctic ecosystems. In Chapter 1, I discussed general characteristics of snow crab and described the ecosystems where they reside. Chapter 2 details a regression modeling study that sought to explain the high recruitment variability of snow crab. The latter study examined the effects of cod predation, climate variability, and spawning stock biomass on the early life history of snow crab in three ecosystems: the eastern Bering Sea (EBS), the southern Gulf of St. Lawrence (SGSL) and in two regions of the Newfoundland-Labrador Shelf (NL). I began by asking four questions and below I provide short answers:

1) Does snow crab recruitment show an inverse relationship with the biomass of gadid predators?

   No. In general, modeling results were not consistent with a predation effect. Predation was negatively related to recruitment only in one region but not in the other areas modeled. However, predators may have indirect effects on snow crab and top-down controls may become important in the future, particularly if Atlantic cod stocks recover.

2) Is snow crab recruitment significantly related to temperature or to other key climate variables?

Yes. Colder climate conditions were associated with increased snow crab recruitment or abundance in subsequent years for all of the ecosystems studied.

3) What effect does adult spawning stock biomass have on future snow crab recruitment?

Spawning stock biomass was not significantly related to recruitment in two regions. And contrary to expectations, when spawning stock biomass was significantly related to recruitment, the relationship was negative. The reasons for this negative relationship are not currently known.

4) Do snow crab show similar relationships with biotic and environmental variables across systems?

Yes. Environmental variability was linked to snow crab populations in all of the subarctic ecosystems studied. However, the role of predation and spawner effects is not clear.

The questions above address how spawner abundance, predation by gadoid fishes, and environmental variability related to temperature influence production and early life survival in snow crab. There are several additional factors that may influence survival of snow crab zoeae, megalopae, or juveniles including wind-driven advection and mixing, cannibalism, and disease or parasitism.

The strength, direction, and timing of wind may impact larval advection in both snow crab (Parada et al. 2010) and its congener, Tanner crab (*Chionoecetes bairdi*) (Rosenkranz et al. 2001). Patterns of larval transport may cause larvae released in some areas to be retained more so than those released in other areas (Parada et al. 2010). Wind-driven advection can carry larval crab to favorable or unfavorable settlement substrates, therefore influencing spatial distribution and early life survival (Rosenkranz et al. 2001). Additionally, as wind conditions vary, so too can nutrient availability and production of prey items available to larvae (Rosenkranz et al. 2001).

Cannibalism, though not directly considered in the models used earlier, has the potential to exert great influence on recruitment strength. Snow crab in Northwest Atlantic Fisheries Organization (NAFO) Division 3K consume other crabs, including smaller conspecifics (Squires & Dawe 2003). Lovrich and Sainte-Marie (1997) examined stomachs of immature, adolescent, and adult snow crab collected from the Gulf of St. Lawrence for the presence of conspecifics. Instars V, VI, and VII represented most of the snow crab eaten indicating that in the first four years after settlement cannibalism by larger crab on smaller crab can reduce cohort strength (Lovrich & Sainte-Marie 1997). Sainte-Marie and Lafrance (2002) conducted a laboratory experiment to examine cannibalism within and between cohorts. Instar I crab had similar survival rates regardless of stocking density. But, when older instar V crab were present the survival rates of the instar I crab decreased. The instar I crab also delayed molting in the presence of the older instar V crab. Their findings suggest that during early benthic stages

predation by older cohorts regulates year class strength more than intracohort cannibalism or competition (Sainte-Marie & Lafrance 2002).

Intracohort cannibalism, if it is a major source of mortality for young crab, has the potential to lead to density-dependence in recruitment such that recruitment is reduced at high spawner abundances. This, along with predation by adults on juvenile stages, could contribute to the observed negative relationship between spawner abundance and recruitment seen in the EBS and a similar (non-significant) relationship seen in NAFO Division 3L. Furthermore, cannibalism by older cohorts may explain the cyclical patterns in residuals. It has previously been hypothesized that endogenous cycles in snow crab populations could result from cannibalism or alternatively from resource limitation (Sainte-Marie et al. 1996). If older crabs have negative density-dependent effects on the newly settled crab then one would expect for successful year classes to be spaced apart such that a large year class must leave the settlement area before another can occur (Sainte-Marie et al. 1996).

Disease and parasitism may also influence snow crab recruitment. The dinoflagellate *Hematodinium* sp. parasitizes snow crab and its congener Tanner crab. Infected crab develop an infection known as bitter crab disease or bitter crab syndrome. For naturally infected crabs, mortality rates of 100% have been noted (Shields et al. 2005). The disease is present in the EBS (Meyers et al. 1996) and in several areas of NL including NAFO Divisions 3K and 3L (Mullowney et al. 2011) but is not yet present in the SGSL stock. Infection has been seen in juvenile Tanner crab in the EBS, though impacts to year-class strength are not well known (Bower et al. 2003). Along the

Newfoundland Shelf, disease prevalence was highest in small snow crab less than 70 mm carapace width and consistently occurred in over 10% of the crabs sampled in the 25 to 40 mm size class (Shields et al. 2005). Bitter crab disease might impact recruitment by diminishing early life survival. Moreover, the disease may interact with climate conditions because its range and prevalence had increased coinciding with warming trends (Morado et al. 2010). Research by Siddeek et al. (2010) indicated that in Tanner crab current management rules may not be sufficient to account for bitter crab disease in a heavily infected stock. Therefore if warming temperatures, or another factor, caused disease prevalence to increase it could become a serious concern for snow crab stocks.

In conclusion, although a variety of factors may influence snow crab survival and recruitment, this study suggests that ocean climate is a dominant driver in the systems and over the time periods examined here. The important role of temperature conditions for snow crab recruitment implies that snow crab will be highly sensitive to future climate warming and the results of my analyses will be useful in quantifying their responses to such warming.

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